

PHOTOSYNTHETIC STRATEGIES OF TWO MOJAVE DESERT SHRUBS

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ABSTRACT.— Photosynthetic production of two Mojave Desert shrubs was measured under natural growing conditions at UCLA. Measurements of photosynthesis, transpiration, resistances to water vapor flux, soil moisture potential, and tissue water potential were made. *Atriplex canescens* (Pursh) Nutt., a member of the C_4 biochemical carbon dioxide fixation group was highly competitive in growth rate and production during conditions of adequate soil moisture. As soil moisture conditions declined to minus 40 bars, the net photosynthetic rate of *Atriplex* decreased to zero. However, the C_3 shrub species *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. was able to maintain positive net photosynthetic production during conditions of high temperature and extreme low soil moisture through the major part of the season. The comparative advantages of the C_4 versus the C_3 pathway of carbon fixation was lost between these two species as the soil moisture potential declined to minus 40 bars. Desert plants have different strategies for survival, one of the strategies being the C_4 biochemical carbon fixation pathway. However, many of the plants are members of the C_3 group. In this instance, the C_4 fixation pathway does not confer an added advantage to the productivity of the species in the Mojave Desert. Species distribution based on comparative photosynthetic production is discussed.

Desert plant species have evolved specialized strategies for coping with extreme environmental conditions. Drought avoidance and drought resistant plant species exist in the same area, although growth and reproduction may occur at different times during the season. In the Mojave Desert, plant species growth response and productivity is governed principally by moisture relationships (Bamberg et al. 1975, 1976). Photosynthetic production is also related to species differences between age, leaf type, and distribution (Cunningham and Strain 1969, Strain 1969, Bjorkman 1971, Wallace and Romney 1972). In addition, desert plants possess special physiological traits such as low leaf tissue moisture and high osmotic pressure (Kozlowski 1968, 1972, Solbrig and Orians 1977) and temperature adaptation (Bjorkman et al. 1971, Pearcy 1977). Many desert plants carry out most of their photosynthesis during favorable periods of the year when moisture relationships are conducive to growth (Hatch and Slack 1970, Jarvis 1971, Caldwell et al. 1972).

Three biochemical pathways for carbon dioxide fixation have been documented rather extensively (Hatch et al. 1971, Burris and Black 1976). These three pathways in-

clude C_3 , C_4 , and CAM photosynthesis. *Atriplex canescens* (Pursh) Nutt., one of the plant species of interest, is a member of the C_4 photosynthesizing group. The second plant, *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., has the C_3 pathway of photosynthesis. There is some consensus of opinion that the C_4 pathway of photosynthesis has conferred some adaptive advantage to species possessing it, enabling them to be more competitive under extreme conditions such as exist in desert environments. In C_4 species, carbon dioxide is first fixed by PEPcarboxylase into aspartate or malate and then transferred to specialized bundle sheath cells for fixation by ribulose diphosphate carboxylase. In C_3 plants, which lack the specialized bundle sheath tissue, carbon is fixed by ribulose 1:5-diphosphate carboxylase. The affinity of the PEPcarboxylase for carbon dioxide is greater than is the affinity of carboxylase for carbon dioxide in the C_4 pathway. Another advantage is a high water use efficiency intrinsic to those plants that have the C_4 pathway. This higher rate of photosynthesis and higher water use efficiency, coupled with higher light saturation and lack of photorespiration, should confer upon those plant species a bet-

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ter adaptive strategy for survival in extreme conditions of the desert (Hatch et al. 1971, Solbrig et al. 1977). It became of interest to study the photosynthetic strategy of two shrubs, one of the C_4 group, *A. canescens*, and one of the C_3 group, *L. tridentata*. The morphology, distribution, and density of the species have been described earlier (Wallace and Romney 1972, Solbrig et al. 1977).

MATERIALS AND METHODS

This work was done on species from the Nevada Test Site located in a transition zone between the Great Basin desert and the Mojave Desert. Climatic conditions in this area are characteristic of both regions, with extreme summer heat and winter cold. The precipitation generally is less than 125 mm yearly. Both plant species are native to this area, with *L. tridentata* being of higher density than *A. canescens*.

Plant materials as cuttings or whole plants were removed from the desert and transported to the UCLA facility for study. Plants taken from the desert were removed during winter dormancy and transplanted directly into cement-lined growth beds where total soil water availability could be controlled. Plant material, as cuttings, was rooted in a glasshouse and then transplanted into the beds for study. The cement-lined beds were 1 × 4 m and 40 cm deep. These growing conditions provided a means for establishing and monitoring plant growth during several seasons. Four beds were used; 6 to 8 plants of each species were used in the study, and numerous photosynthetic measurements were taken on each plant. Soil moisture was measured with psychrometers purchased from Wescor, Logan, Utah. Plant moisture potential was measured with a pressure bomb (Scholander et al. 1965). Gas exchange was measured using a Seamens Null-point chamber as described by Koller (1970). The Seamens equipment was designed to measure CO_2 exchange and transpiration at controlled or ambient conditions. Plant materials previously established in the beds were maintained in a well-watered condition before measurements were taken. Soil water depletion occurred by allowing the plants to utilize the available soil water. Photosynthesis

and transpiration measurements were followed during several drying cycles.

RESULTS AND DISCUSSION

Data presented here are averages of the photosynthetic rates of the two shrub species in two years. Figures 1 and 2 show the comparison of photosynthetic rate and resistance to water vapor diffusion as plotted versus increasing soil water potential for 1974 and 1975. At higher water potentials and higher water availability, *A. canescens* showed higher maximum net photosynthetic rates than *L. tridentata* for both years. The net photosynthetic rate of *A. canescens* was maximum at high soil water content and decreased from near 50 mg CO_2 per square decimeter per hour to near zero as the soil moisture decreased to minus 45 bars. At high soil moisture these data show the *A. canescens* response to be consistent, with C_4 photosynthesis being greater than C_3 ; however, the C_4 advantage is not as apparent at decreasing soil moisture. Data for *L. tridentata* for the two years show the initial lower maximum rate of photosynthesis, but maintenance of a small but positive net CO_2 uptake as the soil moisture decreased to minus 50 bars. *Larrea tridentata* is capable of small positive net photosynthesis during portions of the day to minus 65 bars of soil water potential (Bamberg et al. 1975).

Figure 3 shows the net carbon dioxide uptake of *A. canescens* and *L. tridentata* during morning and afternoon conditions. The C_4 plant, *A. canescens*, shows a higher maximum and a broader range of morning fixation (Fig. 3b) than the C_3 plant, *L. tridentata*. A decreasing rate of photosynthesis and increasing resistance values characterized both plants as soil moisture decreased. The afternoon carbon fixation by *A. canescens* showed a different pattern, i.e., a decrease from an initial high rate at high water content of the soil to a rather low rate. *Larrea tridentata*, on the other hand, showed very little difference between morning and afternoon fixation rates, starting at a maximum of 30 to 35 mg CO_2 per square decimeter, decreasing with decreasing water potential of the soil, but maintaining a positive net fixation to minus 50

bars. Morning measurements of leaf resistance to water vapor flux showed an increase in the afternoon as temperatures gradually increased. Afternoon temperature measurements are commonly 30 to 40 C at UCLA, where the measurements were made. These data show the opposing photosynthetic strategies of the two desert shrubs. The C_4 plant, *A. canescens*, had a higher photosynthetic rate during conditions of lower morning tem-

peratures and higher soil water potentials. However, the C_3 plant, *L. tridentata*, was capable of maintaining a positive net photosynthetic rate at higher stress levels.

In Figure 4, data are plotted which describe the net carbon dioxide uptake at two temperatures, 25 and 35 C. In both species at 25 C, photosynthesis and transpiration paralleled each other as tissue water potential declined. At 35 C transpiration increased pro-

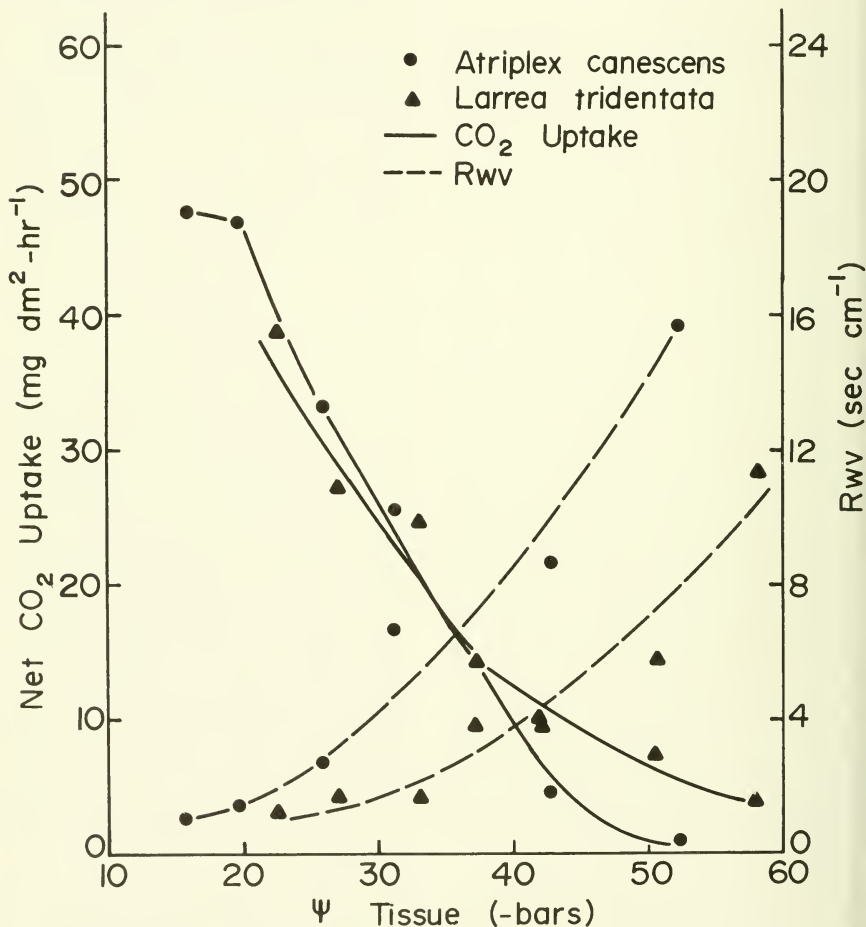


Fig. 1. Daily average rate of photosynthesis and stomatal resistance versus tissue water potential of *Atriplex canescens* and *Larrea tridentata*, 1974. Plants were well established in cement lined beds containing native desert soil. Data represent averages of 20 or more measurements on six plants.

portionately greater than the photosynthetic increase in both species. As the tissue water potential decreased to minus 40 bars at 35 C, the net photosynthetic rate decreased to zero in *A. canescens*. The evergreen shrub, *L. tri-*

dentata, was able to maintain a small but positive net photosynthetic rate as the tissue potential decreased below minus 50 bars.

The photosynthesis to transpiration ratio, as plotted in Figure 5, shows some interesting

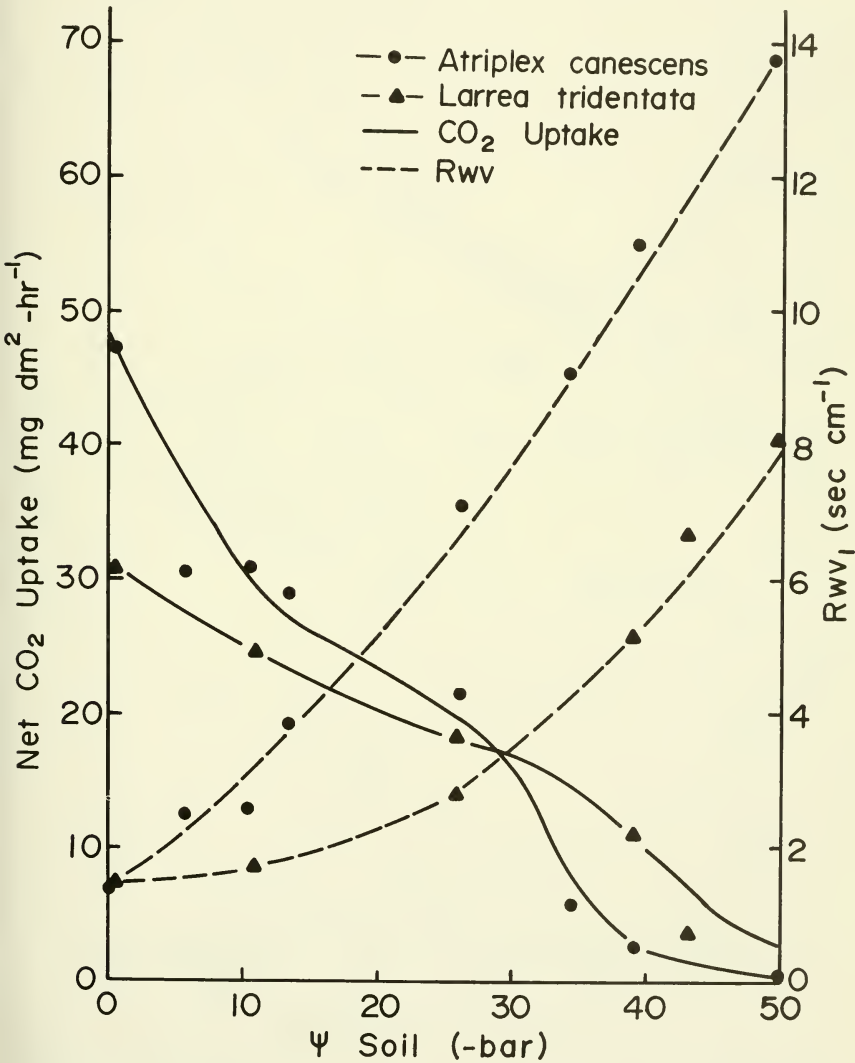


Fig. 2. Daily average rate of photosynthesis and stomatal resistance versus soil water potential of *Atriplex canescens* and *Larrea tridentata*, 1975. Conditions were as described in Figure 1.

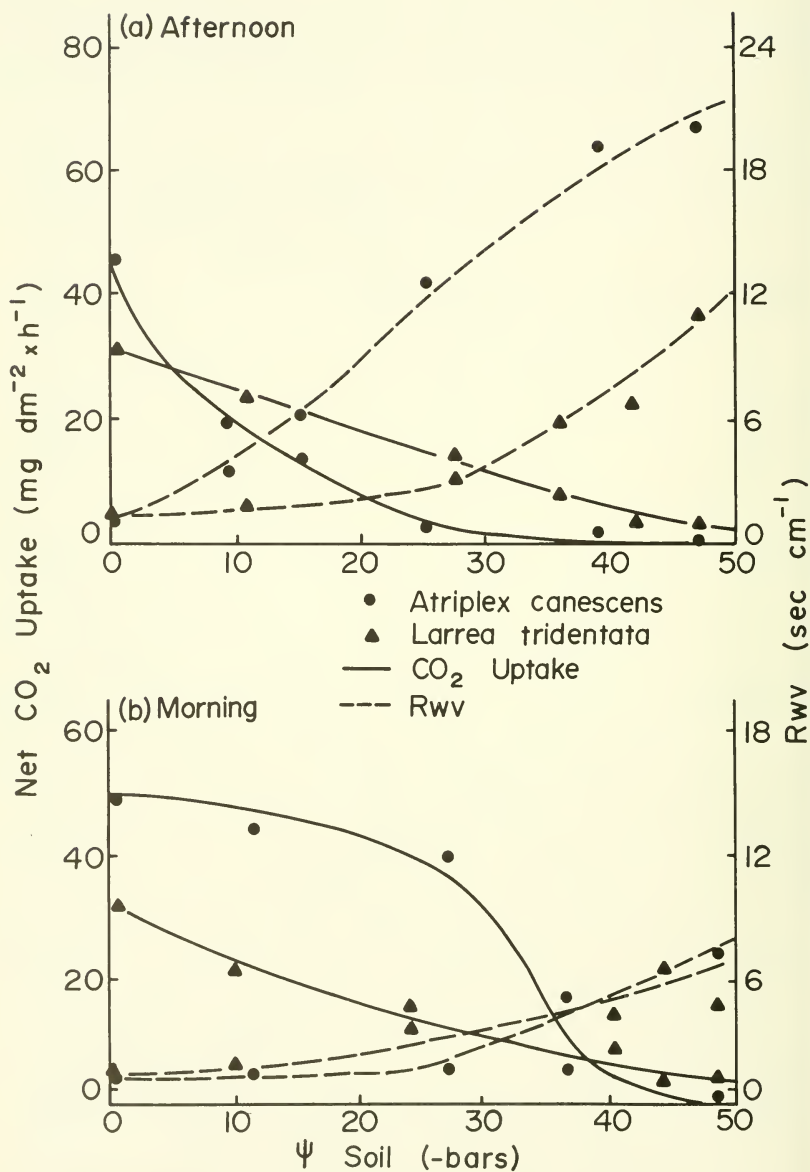


Fig. 3. Photosynthesis and stomatal resistance of two desert shrubs. Data represent averages of plants to morning (cool) conditions and (warm) afternoon conditions as soil moisture declines. Conditions were as described in Figure 1.

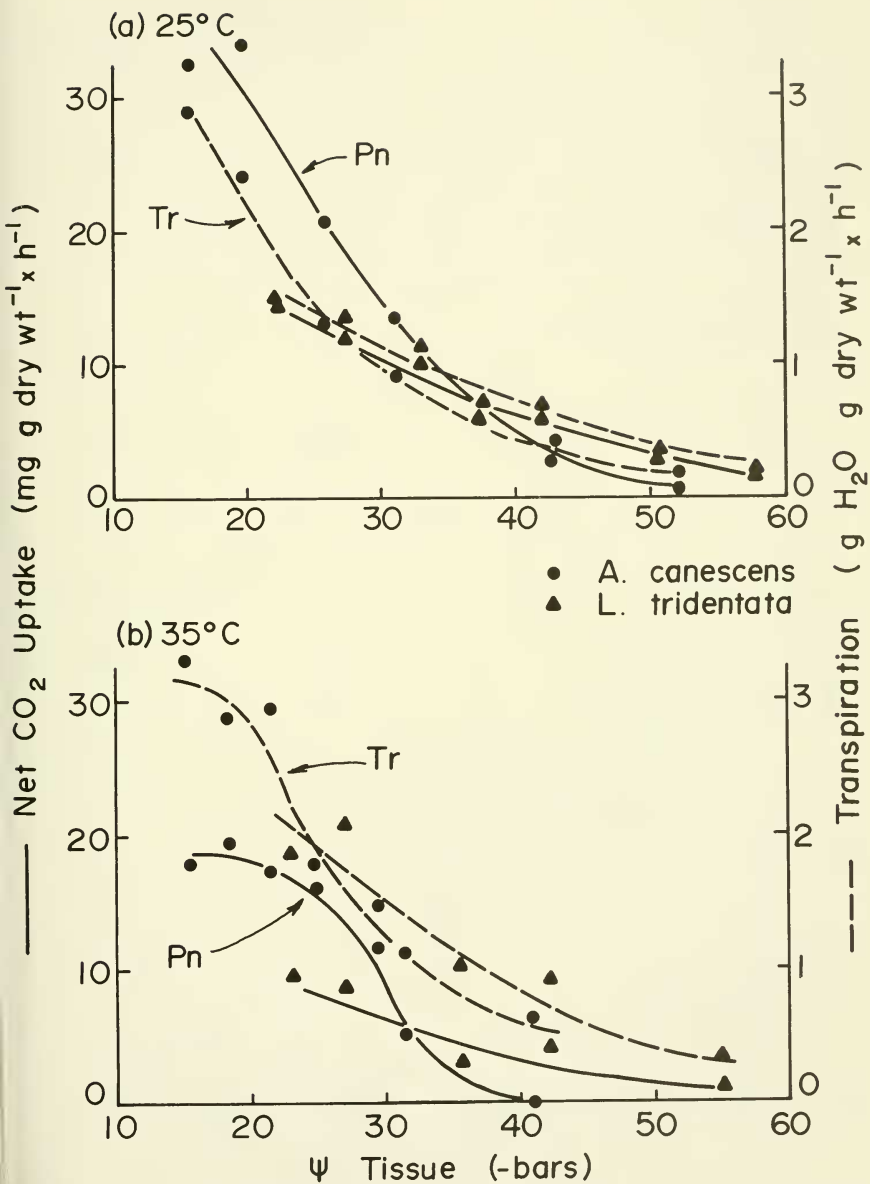


Fig. 4. Daily average rate of photosynthesis and transpiration of two desert shrubs versus tissue water potential at two temperatures. Conditions were as described in Figure 1.

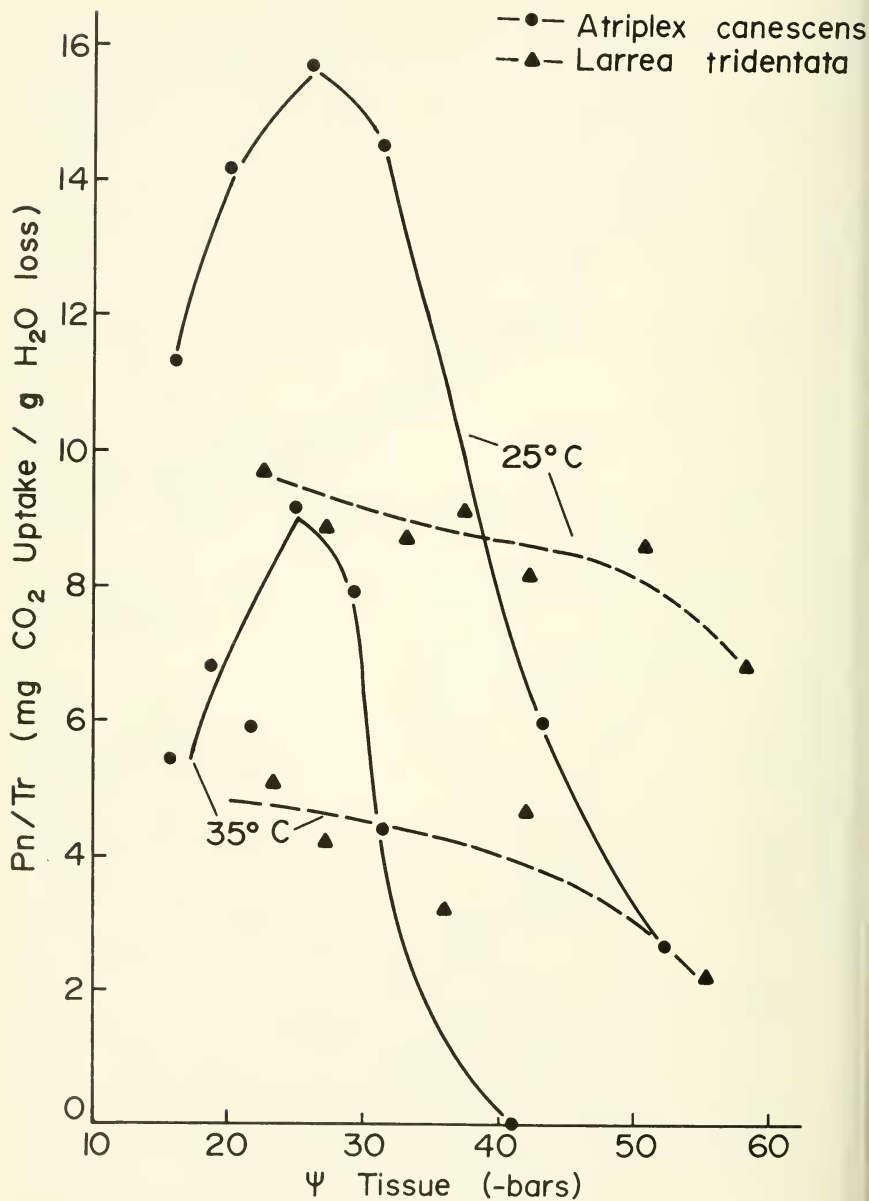


Fig. 5. Water use efficiency versus tissue water potential of two desert shrubs. Experimental conditions are as described in Figure 1.

differences between the C_4 species, *A. canescens*, and the C_3 species, *L. tridentata*. At moderate tissue water potential between minus 10 and minus 30 bars, *A. canescens* showed an increasing water use efficiency at both temperatures 25 C and 35 C. Such is characteristic of a C_4 shrub. However, as the tissue water potential decreased below minus 30 bars, the ratio decreased rapidly. The strategy displayed by the C_3 plant, *L. tridentata*, was somewhat different. The water use efficiency as shown by the photosynthesis:

transpiration ratio decreased rather gradually as tissue water potential declined to minus 50 bars.

Figures 6 and 7 show the relationship between the milligrams carbon dioxide fixed on an area basis and a dry weight basis. These two curves indicate that it is possible with a high degree of confidence to make a dry weight measurement on the leaves and convert that to an area base measurement for resistance calculation. These data also imply that the specific leaf weight of *A. canescens*

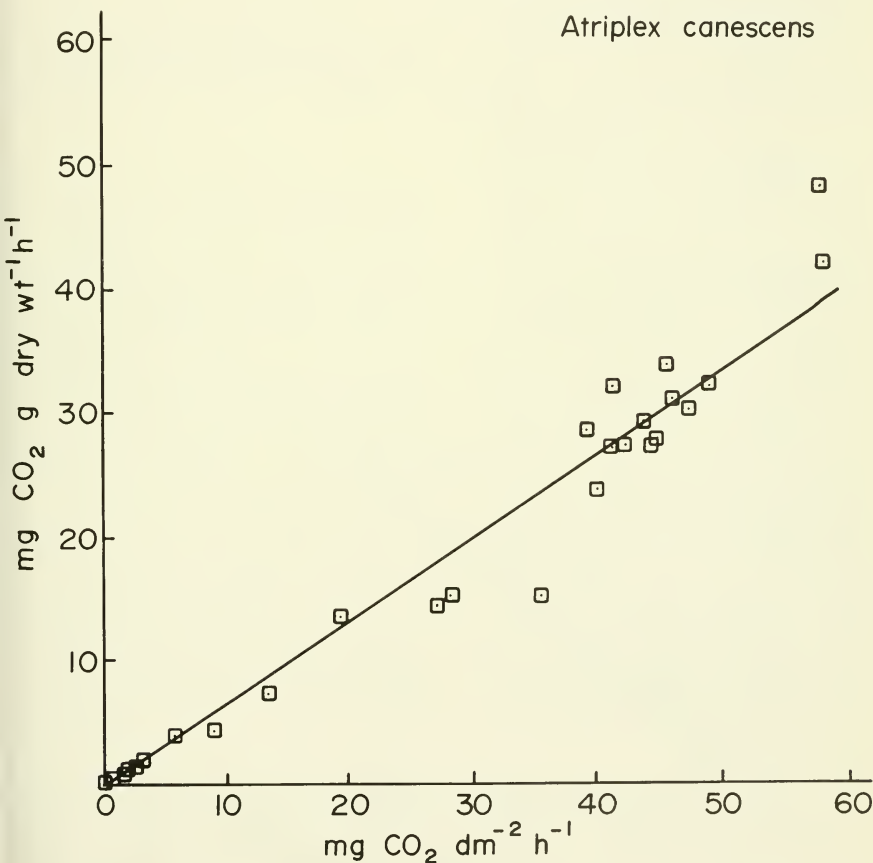


Fig. 6. Photosynthesis of *Atriplex canescens*. Data are plotted to show the correlation between dry weight and leaf surface measurements for a photosynthetic base. Leaf area determinations of numerous small leaves can be time consuming.

and *L. tridentata* do not change as the photosynthetic rates decline due to decreasing water potential of the soil.

These two plant species, one a C_4 carbon fixer and one a C_3 fixer, showed differing strategies in coping with the extreme environment of the desert. The C_4 species, *A. canescens*, appeared to have the higher photosynthetic rate during conditions of moderate moisture and temperature stress. Higher water use efficiency is shown by the C_4 species

under conditions of moderate water stress. However, the evergreen shrub, *L. tridentata*, is capable of maintaining small but positive net photosynthetic rates throughout the major portion of the growing season.

These two plant species differ in their biochemical mechanism of photosynthesis and show contrasting strategies for survival in the desert. *Atriplex canescens* is capable of productivity and growth during a more favorable moisture climate and is not competitive

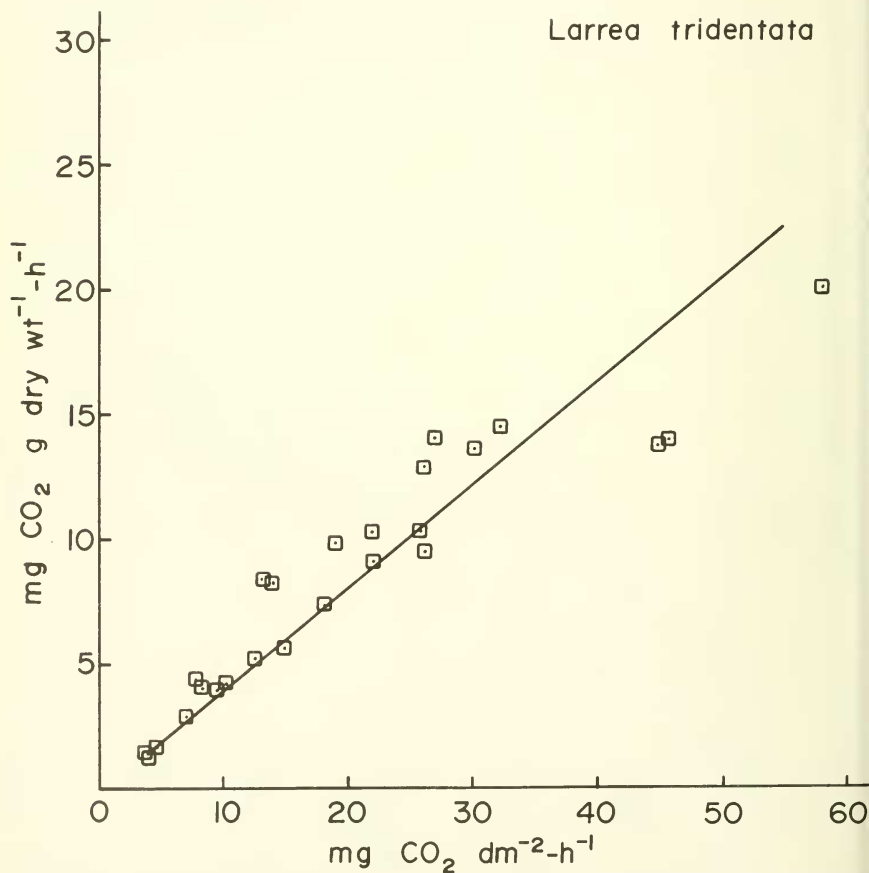


Fig. 7. Photosynthesis of *Larrea tridentata*. Data are plotted to show the correlation between dry weight and leaf surface area.

under soil moisture conditions of less than minus 35 bars. Distribution of the two shrubs in the various desert climates has been described by Wallace and Romney (1972). *Atriplex canescens* appears to be more suitable to the colder, wetter climates provided by the Great Basin desert than does *L. tridentata*. The distribution of *L. tridentata* into the more northern part of the Mojave Desert and into the Great Basin desert appears to be limited by the cold winter temperatures.

ACKNOWLEDGMENTS

This study was supported by Contract EY-76-C-03-0012 between the U.S. Department of Energy and the University of California.

LITERATURE CITED

- BAMBERG, S. A., G. E. KLEINKOPF, A. WALLACE, AND A. VOLLMER. 1975. Comparative photosynthetic production of Mojave Desert shrubs. *Ecology* 56:732-736.
- BAMBERG, S. A., A. T. VOLLMER, G. E. KLEINKOPF, AND T. L. ACKERMAN. 1976. A comparison of seasonal primary production of Mojave Desert shrubs during wet and dry years. *Amer. Midl. Nat.* 95:398-408.
- BJORKMAN, O. 1971. Comparative photosynthetic CO₂ exchange in higher plants. Pages 18-32 in M. D. Hatch, C. B. Osmond, and R. O. Slayter, eds. *Photosynthesis and photorespiration*. New York, Wiley-Interscience.
- BJORKMAN, O., R. W. PEARCY, A. T. HARRISON, AND H. A. MOONEY. 1971. Photosynthetic adaptation to high temperatures: a field study in Death Valley, California. *Science* 175:786-789.
- BURRIS, R. H., AND C. C. BLACK, EDs. 1976. CO₂ metabolism and plant productivity. *Proc. 5th Annual Harry Steinbock Symposium*, University Park Press, Madison, Wisconsin.
- CALDWELL, M. M. 1972. Adaptability and productivity of species possessing C₃ and C₄ photosynthesis in a cool desert environment. Pages 27-29 in L. E. Rodin, ed. *Ecophysiological foundation of ecosystem productivity in arid zone*. Int. Symposium, Leningrad.
- CUNNINGHAM, G. L., AND B. R. STRAIN. 1969. An ecological significance of seasonal leaf variability in a desert shrub. *Ecology* 50:400-408.
- HATCH, M. D., C. B. OSMOND, AND R. O. SLAYTER, EDs. 1971. *Photosynthesis and photorespiration*. Wiley-Interscience, New York.
- HATCH, M. D., AND C. R. SLACK. 1970. Photosynthetic CO₂ fixation pathways. *Ann. Review Plant Physiol.* 21:141-162.
- JARVIS, P. G., AND J. CATSKY. 1971. General principles of gasometric methods and the main aspects of installation design. In *Plant photosynthetic production—manual of methods*. Dr. W. Junk N. V. Publishers, The Hague.
- KOLLER, D. 1970. Determination of fundamental plant parameters controlling carbon assimilation and transpiration by the Null-point compensating system. Lab. of Nuc. Medicine and Rad. Biology, University of California, Los Angeles. Report. 12-797.
- KOZLOWSKI, T. E., ED. 1968. *Plant water consumption and response*, Vol. 2. Academic Press, New York-San Francisco-London.
- . 1968. *Development, control, and Measurement*. Vol. 1. Academic Press, New York-San Francisco-London.
- . 1972. *Plant responses and control of water balance*, Vol. 3. Academic Press, New York-San Francisco-London.
- PEARCY, R. W. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.) Wats. *Plant Physiol.* 59:797-799.
- SCHOLANDER, P. F., E. D. BRADSTREET, H. T. HAMMEL, AND E. A. HEMMINGSON. 1965. Sap pressure in vascular plants. *Science* 148:339.
- SOLBRIG, O. T., AND G. H. ORLANS. 1977. The adaptive characteristics of desert plants. *American Scientist* 65:412-421.
- SOLBRIG, O. T., M. BARBOUR, J. CROSS, G. GOLDENSTEIN, C. LOWE, J. MORELLO, AND T. W. TANG. 1977. The strategies and community patterns of plants. In G. H. Orlans and O. T. Solbrig, eds. *Convergent evolution in warm desert ecosystems*, Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania.
- STRAIN, B. R. 1969. Seasonal adaptations in photosynthesis and respiration in four desert shrubs growing in situ. *Ecology* 50:511-513.
- WALLACE, A., AND E. M. ROMNEY. 1972. Radioecology and ecophysiology of desert plants at the Nevada Test Site. National Technical Information Services, USAEC Report TID-25954.